

FUNCTIONAL COCHLEAR MORPHOLOGY OF THE TWO-TOED SLOTH (*CHOLOEPUS* SP.)

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Abstract

A morphometric study of the cochlea was made from serial sections and graphic reconstructions of the cochlea of two-toed sloths. The cochlea had 2-1/4 spirals and measured approximately 17.4 mm in length. Cochlear morphometric parameters studied were the changes in cross-sectional area of the scalae vestibuli, media, and tympani, thickness of the pars tecta and the pectinata of the basilar membrane, width of the basilar membrane, and density of the bipolar ganglion cells. The change in the cross-sectional area of the scala vestibuli differed from the scala tympani; the former decreased from the oval window and increased to a second maximum value at 12.2 mm from the basal end, while the latter increased from the round window membrane to a maximum value at 4.8 mm and remained unchanged throughout the remainder of the cochlear length. The cross-sectional area of the scala media remained relatively constant throughout the cochlear length. There was a fourfold increase in the change of the width of the basilar membrane from base to apex. There was a gradual increase in width from the base to 12.2 mm followed by a steep increase to a maximum value of 275 μ m before it declined to the apex. There was little change in the thickness of the pars tecta and the pars pectinata of the basilar membrane from the base to 8.5 mm before it declined at the apex. These morphometric features indicated a distinct region of morphological discontinuity 10.5 - 13 mm along the length of the basilar membrane. Within this region the stiffness gradient was greatest, and the theoretical position of maximum amplitude of vibration for the frequencies 0.5-1.5 kHz, also coincided. There were 19,900 bipolar-ganglion cells enumerated and the greatest density occurred at 13 mm where 1,600 cells/mm² were present. These morphological findings correlate with the known psychoacoustic data on the two-toed sloth.

Abstracto

Se llevó a cabo un estudio morfométrico de la cóclea por medio de secciones en serie y de reconstrucciones gráficas de cócleas de perezosos de dos dedos. La cóclea tenía 2-1/4 espirales y medía aproximadamente 17.4 mm de largo. Los parámetros morfométricos estudiados fueron los siguientes: los cambios en el área de corte transversal de las escalas de los vestíbulos, de las medias y de los tímpanos; el espesor de las pars tecta y pars pectinata de la membrana basilar; el ancho de la membrana basilar, y la densidad de las células del ganglio bipolar. El cambio en el área transversal de la escala del vestíbulo fue distinto al de la escala del tímpano; el primero de ellos decreció desde la ventana oval y aumentó a un segundo valor máximo, a una distancia de 12.2 mm de la extremidad basal, mientras que el segundo aumentó desde la membrana redonda de la ventana hasta un valor máximo a una distancia de 4.8 mm y permaneció sin cambios por el resto de la longitud coclear. El área de corte transversal de la escala media permaneció relativamente constante a lo largo de toda la longitud coclear. Hubo un aumento total de cuatro veces en el cambio, con el ancho de la membrana basilar desde su base hasta el ápice. Hubo un aumento gradual en el ancho hasta una distancia de 12.2 mm de la base, seguido por un aumento brusco hasta un valor de 275 μ m, antes de declinar hasta su ápice. Hubo muy pequeños cambios en el espesor de la pars tecta y de la pars pectinata desde la membrana basilar hasta una distancia de 8.5 mm de su base, para luego decrecer hacia sus ápices. Estos rasgos morfométricos indican que una región distinta de discontinuidad morfológica ocurre entre los 10.5 y 13 mm, a lo largo de la longitud de la membrana basilar. Dentro de esta región, fue mayor la gradiente de rigidez; también coincidió la posición teórica de amplitud máxima de vibración para las frecuencias 0.5 - 1.5 kHz. Se enumeraron 19,900 células de ganglios bipolares y la mayor densidad ocurrió a 13 mm, donde había 1,600 células por mm². Estos hallazgos se correlacionan con datos conocidos psicoacústicos del perezoso de dos dedos.

Resumo

Um estudo morfométrico da cóclea foi feito de cortes seriados e reconstruções gráficas da cóclea de duas preguiças reais. As duas voltas e meia da cóclea da preguiça mediam aproximadamente 17.4 mm de comprimento. Parâmetros morfométricos cocleares estudados foram as mudanças; a área do corte transversal da escala vestibular, média e timpânica; na espessura do pars tecta e pectinata da membrana basilar; na largura da membrana basilar; na densidade das células ganglionares bipolares. A mudança na área do corte transversal da escala vestibular diferiu da escala timpânica, o primeiro diminuiu da janela oval e aumentou para um segundo valor máximo de 12,2 mm do final basal, enquanto o último aumentou da membrana da janela redonda para um valor máximo a 4,8 mm e permaneceu inalterado pelo comprimento coclear restante. A área do corte transversal da escala média permaneceu relativamente constante por todo o comprimento coclear. Houve um aumento geral de quatro vezes na mudança com a largura da membrana basilar, da base ao ápice. Houve um aumento gradual na largura da base para 12,2 mm seguido por um abrupto aumento a um valor máximo de 275 μ m, antes de

declinar para o ápice. Há uma pequena mudança na espessura do pars tecta e do pars pectinata da membrana basilar da base para 8,5 mm, antes de declinar no ápice. Esses aspectos morfométricos indicaram que uma região distinta de descontinuidade morfológica ocorreu entre 10,5 - 13 mm ao longo do comprimento da membrana basilar. Dentro dessa região o gradiente de dureza foi o maior e a posição torácica da amplitude máxima de vibração para as frequências 0,5 - 1,5 KhZ também coincidiram. Houve 19.900 células ganglionares bipolares enumeradas e a mais alta densidade ocorreu a 13 mm, onde havia 1.600 células/mm³. Esses achados morfológicos se correlacionam com os dados psicoacústicos conhecidos na preguia real.

This report is concerned primarily with the morphometrics of the cochlea of the two-toed sloth. Recently there has been a revival of interest in the morphology of the mammalian cochlea. One outcome of this revival has been the attempt to correlate the neuroanatomical data, and psychoacoustic data to the morphometric parameters studied within the cochlea itself (Bruns, 1976a, 1976b; Ehret and Frankenreiter, 1977; Ramprasad et al., 1979). It is within the cochlea that sound is transformed into neural impulses by the stimulation of the mechanoreceptors (sensory hairs) of the organ of Corti.

Precise psychoacoustic data in some Xenarthra (= Edentata) have been determined by Suga (1967), and Peterson and Heaton (1968). Suga (1967) has shown that the frequency range of hearing of the xenarthran audiogram was of the order of 0.3-25 to 30 kHz, with the region of greatest sensitivity occurring at 2-8 kHz at 100 db SPL. Peterson and Heaton (1968) showed that the maximum cochlear-microphonic output of 250 μ V occurred between frequencies of 0.5-3 kHz. Both studies confirmed that xenarthran hearing was somewhat inferior to that in other terrestrial mammals. Contact-distress calls emitted by young sloths were in the frequency range of 2.0 kHz, i.e., between 1.9-2.6 kHz for the three-toed sloth and 1.4 kHz for the two-toed sloth (Montgomery and Sunquist, 1974). It would be most informative if the morphometric parameters and the neuroanatomical data within the sloth cochlea could be correlated with the psychoacoustic data.

What is known about the structure of the sloth ear indicates that, apart from a few primitive features, it possesses no peculiar structural features, i.e., it is typically mammalian (Weber, 1928; Neubert and Wustenfelf, 1926; Demanez et al., 1968). Primitive features mentioned were: (a) the wall of the osseous external auditory meatus consists of a narrow semicircular annulus tympanicus which is directed upwards and backwards (a feature also found in monotremes, marsupials, insectivores, chiropterans, sirenians and lemurs), (b) the stapes is "columellarlike" (Fig. 2), (c) the lack of insertion of the *tensor tympani* muscle onto the malleus, and (d) the peculiar shape of the tympanic membrane (Goffart, 1971). Half-coil measurements of the cochlear height, number of half turns, cochlear width, and the width and thickness of the basilar membrane of the xenarthran cochlea have been provided in a recent study (Pye, 1979). However, detailed morphometric information is lacking for the xenarthran cochlea. The prime purpose of this report is to elucidate the morphometric



Figure 1. Photomicrograph of a sagittal section through middle ear showing the malleo-incudal joint. (M) - malleus, (I) - incus, (F.P.) - foot plate of the stapes, (S.M.) - stapedius muscle. Scale bar = 255 μ m.

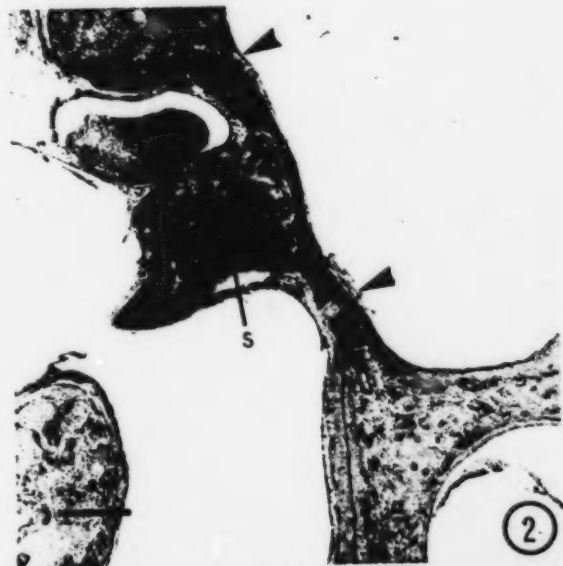


Figure 2. Photomicrograph of a horizontal section through the middle ear showing the primitive "massive" columellar type stapes (S) within the oval window. Note the rather large annular ligament at the arrows, and the absence of an intercrural space. Scale bar = 255 μ m.

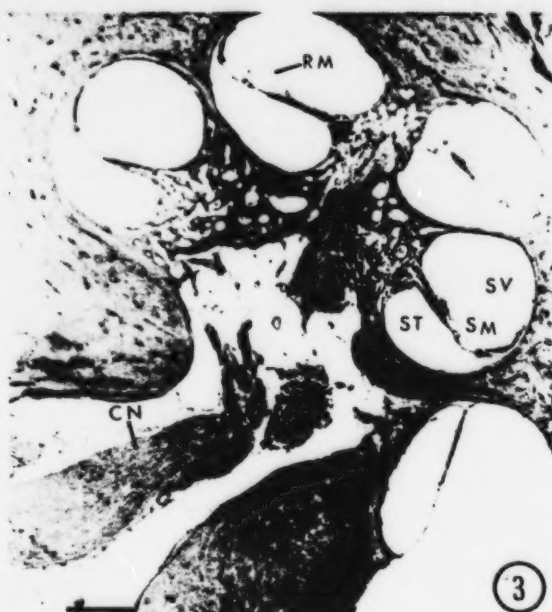


Figure 3. Low power photomicrograph showing the general features of the cochlea of the sloth. Shown are the cochlear nerve (C.N.) entering the bony modiolus, the two and a quarter turn cochlea, (S.V.) - scala vestibuli, (S.M.) - scala media, (S.T.) - scala tympani, and (R.M.) - Reissner's membrane. Scale bar = 255 μ m.



Figure 4. Low power photomicrograph showing the bifurcation of the cochlear nerve into the basal branch (b.b.) which innervates the basal coil only, and the position of the spiral ganglion (S.g.). Illustrated also are (V.G.) - vestibular ganglion, and (Sa) - saccule with its sensory epithelium, the macula sacculi at the arrows. Scale bar = 255 μ m.

parameters which could provide some insight into the cochlear mechanics of the two-toed sloth (*Choloepus* sp.).

COCHLEAR MORPHOLOGY

The cochlea of the sloth is typically mammalian. The bony cochlea is a helical tube, the cochlear canal, which forms about two-and-a-quarter turns (Figs. 3, 4). Within the cochlear canal is the membranous organ of Corti. The cochlear canal spirals around the modiolus, a central axis of spongy bone. The modiolus is perforated by numerous bifurcations of the auditory nerve (Fig. 4).

The lumen of the cochlear canal is partially subdivided by a thin plate of bone extending from the modiolus, the osseous spiral lamina, into an upper scala vestibuli and a lower scala tympani; both of which are part of the perilymphatic system (Figs. 3, 4). The scala vestibuli starts from the oval window into which fits the footplate of the stapes, it then spirals upwards and, at the apex of the cochlear canal, joins the scala tympani through a narrow connection, the helicotrema. The term "upwards" refers to an ascending direction in the plane of the cochlear axis. A direction following the course of the cochlear canal is called "spiral" and a radial direction from the axis of the cochlea is called "outwards" (Bredberg, 1968). From the helicotrema, the scala tympani spirals downward and ends posteriorly at the fenestra rotundum.

The fenestra rotundum is closed by a small, thin, fibrous, round window membrane (Fig. 5). The round window membrane functions as a pressure release

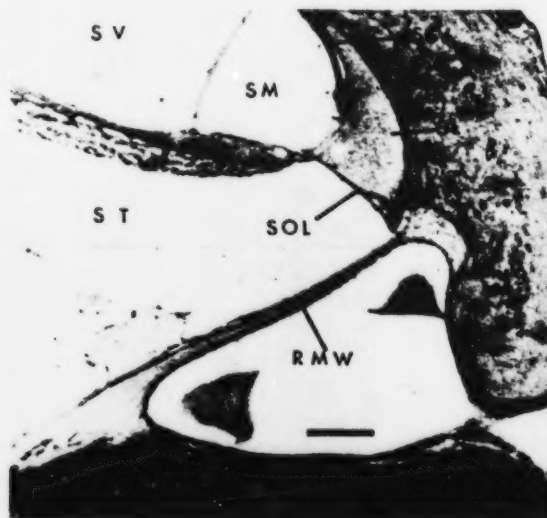


Figure 5. Photomicrograph of a sagittal section at the round window margin of the round window membrane, and the spiral ligament (S.L.) of the organ of Corti. (S.V.) - scala vestibuli, (S.M.) - scala media, (S.T.) - scala tympani, (S.O.L.) - secondary spiral osseous lamina. Scale bar = 255 μ m.

mechanism for the pressure waves imparted on the cochlear perilymph by the movement of the footplate of the stapes. On the medial floor of the fenestra rotundum is the large ovoid orifice of the cochlear aqueduct, which opens into the scala tympani.

The inner part of the cochlear duct is attached to the osseous spiral lamina. The basilar membrane extends from the osseous spiral lamina outwards to the outer bony cochlear wall. The basilar membrane is firmly attached to the outer bony wall by the thickened periosteum, the spiral ligament (Fig. 5). The spiral ligament is more prominent in the lower basal coil of the cochlea especially near the round window membrane (Figs. 3, 4, 5). The outer wall of the cochlear duct is vascularized with a thick epithelium, the stria vascularis, which ends above the basilar membrane as the *prominentia spiralis*.

The cochlear duct (the *scala media*) is triangular when sectioned in the mid-modiolar plane (Figs. 3, 4, 5). Reissner's membrane separates the *scala vestibuli* from the *scala media*, and the horizontal basilar membrane separates the *scala media* from the *scala tympani*. Above the osseous spiral lamina the periosteum is thickened into the spiral limbus, which extends outwards into the cochlear duct; the tectorial membrane is attached to the vestibular lip of the spiral limbus. In vivo, the tectorial membrane extends over the organ of Corti. The tectorial membrane and the tympanic lip of the spiral limbus enclose the spiral tunnel.

Above the basilar membrane is the specialized organ of Corti (Figs. 6, 7). There are the characteristic inner and outer pillar cells, between which is the inner tunnel (tunnel of Corti). The nuclei of the pillar cells are found in the broad base of the cells above the basilar membrane (Fig. 7).

Medial to the inner pillar cell is a row of inner phalangeal cells which support a single row of inner hair cells (Fig. 7). Outwards from the outer pillar cells are the phalangeal "Deiters" cells which support the outer 3-4 rows of hair cells (Figs. 6, 7). The outer hair cells are cylindrical and the inner hair cells are pear-shaped (Fig. 7). Stereocilia (but no kinocilium as in other mammals) project from the apices of the hair cells into the tectorial membrane.

The hair cells are connected together apically by a thin reticular membrane. It is these hair cells that are the mechanoreceptors which act as transducers for sound energy into nerve impulses. The maximum amplitude of vibration for a particular frequency occurs at a specific location along the length of the membrane (Bekesy, 1941, 1956).

Changes in the cross-sectional area of the scalae.—Present understanding of hearing in mammals is based on the premise that the acoustical energy, which is transmitted across the ossicular chain, is transformed into hydro-

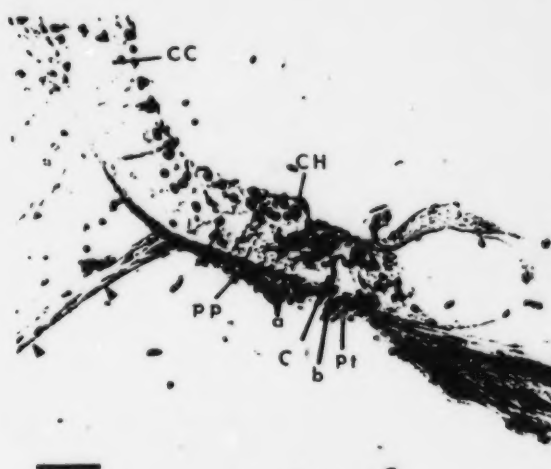


Figure 6. Photomicrograph of a horizontal section of the cochlea at approximately 1.5 mm from the basal end. Note the features of the organ of Corti: the large cells of Hensen (C.H.), and the cells of Claudius (C.C.). Note the absence of a secondary osseous lamina at arrows within the spiral ligament, a feature which is characteristic of low-frequency-hearing mammals. The limits of the pars tecta (p.t.) and pars pectinata (p.p.) are delineated by the outer pillar cell at C (a and b are shown in greater detail in Fig. 11). Scale bar = 26 μ m.

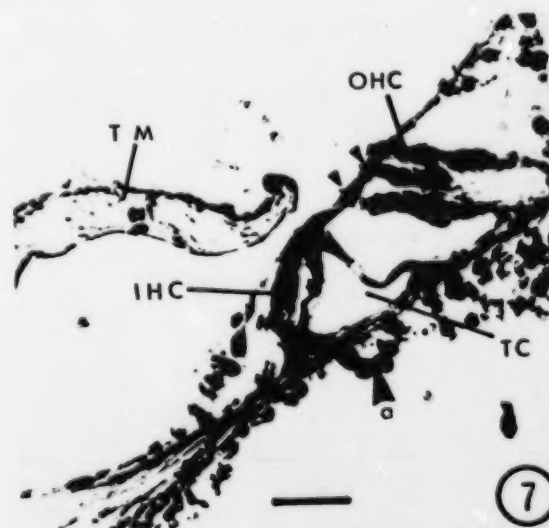


Figure 7. Photomicrograph showing typical mammalian structure of the sensory epithelium of the sloth. Note the appearance of the inner hair cells (I.H.C.), the three rows of outer hair cells (O.H.C.) and the stereocilia at the arrows. Note also the vas spirale at arrow (a) within the pars tecta. (T.M.) - tectorial membrane, (T.C.) - Tunnel of Corti. Scale bar = 11 μ m.

dynamic movements of the cochlear perilymphatic and endolymphatic systems thus creating a travelling wave along the length of the basilar membrane (Bekesy, 1941; 1948; 1956). Therefore, measurements of the

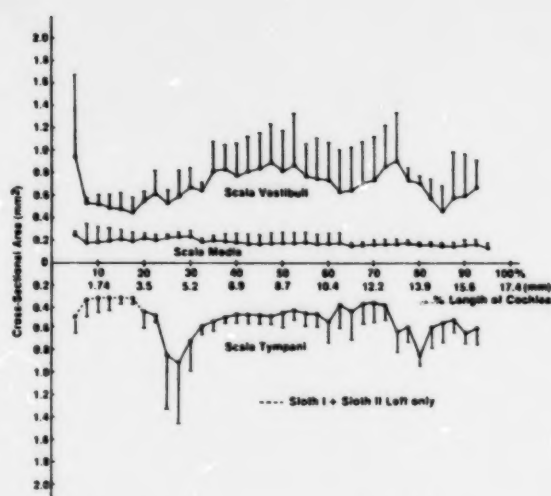


Figure 8. Changes in the cross-sectional area of the scalae vestibuli, tympani and media along the cochlear length. Dots and vertical bars represent means and SD. Note (i) the relatively small change in the scala media along the cochlear length (ii) the rapid decrease in cross-sectional area of the scala vestibuli, (iii) the decreased cross-sectional area between 1-2 mm in the scalae vestibuli and tympani, (iv) the increase in cross-sectional area in the scalae vestibuli and the tympani between 12-13 mm.

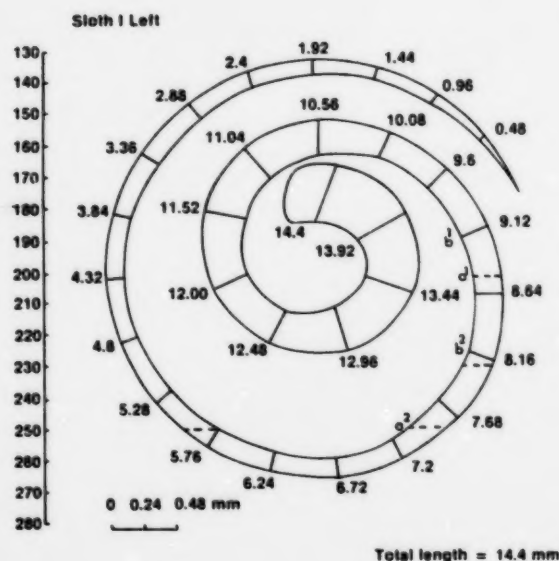


Figure 9. Change in width of the basilar membrane along the cochlear length. Graphic representation of the cochlea follows the procedure of Guild (1921). The widths at b^1 , b^2 , etc. are taken from a slide in a serial series whose numbers are shown to the left of the figure. Radial lines a^1 , a^2 are the true width corrected for the plane of sectioning (Ramprasad, et al., 1979). Note that the cochlea is approximately a two and a quarter turn spiral. Since no measurement was obtainable, the extreme basal end is represented as zero width.

cross-sectional area of the scalae and the width and thickness of the basilar membrane can provide useful information on the cochlear mechanics of the two-toed sloth.

The cross-sectional area of the scala vestibuli is largest at the oval window where it measures 1.6 mm^2 , then it decreases to 0.5 mm^2 at 0.5 mm before increasing to a second maximum of 0.9 mm^2 at 12.2 mm . From there, it decreases to the apex of the cochlea (Fig. 8).

The change in cross-sectional area of the scala tympani differs from that of the scala vestibuli (Fig. 8). At the round window membrane, its cross-sectional area measures 0.6 mm^2 , then it increases to a maximum of 1.0 mm^2 at 4.8 mm , following which it returns to approximately 0.6 mm^2 for the remainder of the length of the cochlea.

The change in the cross-sectional area of the scala media differs from that of the other two scalae. The cross-sectional area of the scala media measures approximately 0.2 mm^2 and remains relatively constant throughout the cochlear length (Fig. 8). The cross-sectional area of the helicotrema was estimated to measure approximately 0.25 mm^2 .

Comparative considerations.—Changes in the cross-sectional area of the scalae have been determined in a number of mammals, for instance in the Heteromyid rodents (Webster and Webster, 1977), in the little brown bat (Ramprasad et al., 1979), in the human, and in the guinea pig (Fernandez, 1952).

In all mammals studied thus far, the scala media remains relatively unchanged throughout the cochlear length. Although the trends in the change of the scalae vestibuli and tympani are similar in all mammals, i.e., a decrease in cross-sectional area from base to apex, there are individual species differences. The curves of the sloth are similar in profile to the Heteromyid rodents (Webster and Webster, 1977) in that there is a second maxima in the apical region of the cochlea. In the human and the guinea pig, the cross-sectional areas of the scalae vestibuli and tympani decrease gradually from base to apex (Fernandez, 1952).

Changes in the width of the basilar membrane.—Although the width of the basilar membrane increases from the base to the apex, the change in width occurs in two distinct stages (Fig. 10). There is a gradual increase in width from $70 \mu\text{m}$ at the base to $175 \mu\text{m}$ at 12.2 mm , an increase of 150 percent. Then there is a relatively steep increase, from 175 – $275 \mu\text{m}$ between 12.2 – 14.0 mm , followed by a further increase of 53 percent before it attains a maximum width of $275 \mu\text{m}$ between 14.0 – 15.7 mm . The overall change in width from the base to its maximum width is approximately fourfold.

Comparative considerations.—The change in width of the

basilar membrane along the cochlear length in the two-toed sloth is similar to that of the Heteromyid rodents (Webster and Webster, 1977), and of Microchiroptera (Bruns, 1976a; Henson, 1978; Ramprashad et al., 1979). In all these mammals there is an uneven change in width along the cochlear length. However, the change in width is uniform from base to apex in the human, cat, guinea pig and cetacean (Wever, 1938; Fernandez, 1952; Wever et al., 1971; Cabezudo, 1978). Changes in width of the basilar membrane of some mammals suggest that overall changes in width of the basilar membranes appear to have little association with the frequency ranges of their respective audiograms (Tables 1 and 2). For example, the overall change in cochlear length of the two-toed sloth is approximately 3.8; this is of a greater magnitude than that of the lesser horseshoe bat, *Rhinolophus*. Additionally, these two species have similar basal widths of 17 μ m (Bruns, 1976a). *Rhinolophus* is an echolocating bat which uses

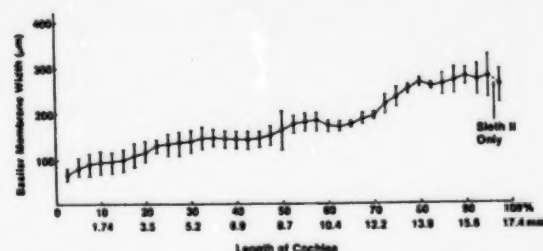


Figure 10. Change in width of the basilar membrane along the cochlear length. Dots and vertical bars represent means and SD. Note that the change in width occurs in two distinct phases; (i) a gradual increase from the base to approximately 10.4 mm, and (ii) a more rapid increase to a maximum of 275 μ m.

constant frequency modulation and is therefore classed as a high frequency hearing mammal.

The hearing range of the sloth is from 0.3 to 30 kHz (Suga, 1967; Peterson and Heaton, 1968). The best

Table 1: Variation in the total cochlear length of mammals with change in the width of the basilar membrane.

Mammal	Cochlear Length (mm)	Basal Width (μ m)	Maximum Width (μ m)	Overall Change	Reference
Little brown bat	6.8	57	115	2.0	Ramprashad et al. 1979
House mouse	6.8	40	150	3.7	Ehret and Frankenreiter 1977
<i>Liomys</i>	9	110	150	1.3	Webster and Webster 1977
<i>Dipodomys</i>	10	90	250	2.8	Webster and Webster 1977
<i>Peteronotus</i>	12	38	80	2.1	Henson 1978
<i>Rhinolophus</i>	17	70	155	2.2	Bruns 1978a
<i>Choloepus</i>	17.1	70	275	3.8	This study
Guinea pig	20	70	250	3.6	Fernandez 1952
Cat	22	106	426	4.0	Cabezudo 1978
Human	32	80	500	6.2	Fernandez 1952
Harp seal	33	90	525	5.8	Ramprashad et al. 1979
Pacific White-sided Dolphin	36	30	300	10	Wever et al. 1971
<i>Tursiops</i>	40	25	350	14	Wever et al. 1972

Table 2: A comparison of the total number of ganglion cells and the range of hearing (kHz) in some mammals.

Mammal	Mean Number of Ganglion Cells	Range of Hearing	Frequency of Echo-Location	Average Body Mass (kg)	Author(s)
Two toed Sloth					
<i>Choloepus</i>	19,900	0.3-30		3.0	Peterson and Heaton 1968
Rabbit	26,700			0.4	Ramprashad et al., 1982
Human	30,500	0.032-20		70	Wever 1949; Schuknecht 1974
Cat	49,962	0.063-52		3.3	Howe 1935; Schuknecht 1974
Harp Seal	52,000	1-32 (air)			Ramprashad 1976;
<i>Pugophilus</i>		0.5-100 (water)		78	Terhune and Ronald 1971, 1972
Little Brown Bat					
<i>Myotis</i>	56,000	0.7-150	25-120	0.005	Ramprashad et al. 1979; Grinnel 1963
Pacific White-sided Dolphin					
<i>Lagenorhynchus</i>	65,000	0.6-80	30-60	95	Wever et al. 1972; Evans 1973
Bottlenose Dolphin					
<i>Tursiops</i>	95,000	1-100	30-69	118	Evans 1973

frequencies for activating the adult sloth ear are in the range 2 to 8 kHz (Suga, 1967). The peripheral auditory function of two-toed sloths is optimized for the range 0.5 to 3 kHz (Peterson and Heaton, 1968). The distress calls of young two-toed sloths are relatively low-pitched, with most of the sound energy concentrated below 1.4 kHz (Montgomery and Sunquist, 1974). It seems likely, that hearing in the adult sloth would be optimized for this range of frequencies, i.e., that these are mammals which hear low frequencies best. Although the sloth's cochlea has typically mammalian features, it lacks a well-developed secondary spiral osseous lamina within the basal coil. This secondary spiral is a characteristic feature found within the cochlea of all high-frequency-hearing mammals, including Microchiroptera (Pye, 1966a, 1966b, 1967; Hall, 1969; Bruns, 1976a, 1976b; Henson, 1978; Ramprashad et al., 1979), Phocida (Mohl, 1968; Ramprashad et al., 1972) and Cetacea (Wever et al., 1971a, b, c, 1972). In the two-toed sloth, the secondary spiral osseous lamina is only present at the round window (Fig. 5). This anatomical feature of the sloth ear is common to other low-frequency-hearing mammals (e.g., the human and the guinea pig.).

Changes in the thickness of the basilar membrane.--The sensory hair cells in the organ of Corti are the transducers of sound energy into nerve impulses. The stimulation of these mechanoreceptors depends entirely on the vibration pattern of the basilar membrane and the subsequent shearing motion of the tectorial membrane and the stereocilia. It follows that morphological discontinuities along the basilar membrane length may alter its physical properties, which would also alter the vibrating properties of the basilar membrane. Therefore, the changes in thickness along the basilar membrane can serve as indicators of the changes of the mechanical and, perhaps, vibrating properties of the basilar membrane.

The mammalian basilar membrane can be arbitrarily divided into two regions, the pars tecta and the pars pectinata (Fig. 6). The outer pillar cell was used as a landmark to delineate the pars tecta from the pars pectinata. The pars tecta and the pectinata are not of uniform thickness throughout the cochlear length (Fig. 11). The pars tecta and the pars pectinata are thickest at 12.6 mm and 9.4 mm, respectively. There is very little change in the overall thickness of the basilar membrane from the base to about 8.0 mm along the cochlear length (Fig. 12). However, it gradually increases and reaches its maximum thickness at 12.3 mm to 12.8 mm before decreasing at the apex. These figures clearly indicate that distinct morphological discontinuities occur along the basilar membrane of the sloth.

Comparative considerations.--Recent morphometric studies on the basilar membrane of bats (Bruns, 1976a, 1976b; Ramprashad et al., 1979), house mice (Ehret and

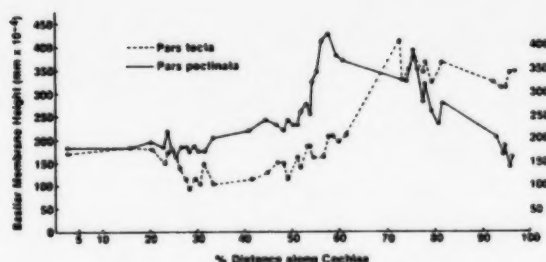


Figure 11. Change in the maximum thickness (height) of the pars tecta and pars pectinata of the basilar membrane. See a, b, in Fig. 6 for reference points which were measured. Note; (i) the similarity of the curves for both pars tecta and pectinata, and (ii) the different position where the maximum thicknesses occur. Dots represent mean values from two temporal bones.

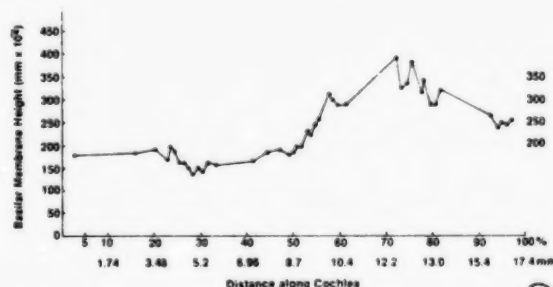


Figure 12. Change in the thickness (average height) of the basilar membrane along the cochlear length. Note; (i) the maximum thickness occurs at 12.2 mm, (ii) the thickness of both the pars tecta and pectinata remain constant from the base to approximately 3.5 mm, (iii) the pars tecta and the pectinata are thicker in the apical region than at the basal end, attributable to the thicker mesothelial layer of the basilar membrane (see Cabezudo, 1978).

Frankenreiter, 1977), and cats (Cabezudo, 1978) show that morphological discontinuities occur along the basilar membrane. The region of morphological discontinuity in the sloth was not as pronounced as in the cat or in the bat. In all mammals studied, the changes in the thickness of the pars pectinata influenced the overall change in the thickness of the basilar membrane. In the Microchiroptera (Pye, 1966; 1966b; 1967; Bruns, 1976a; Ramprashad et al., 1979; Henson, 1978), in the Heteromyid rodent (Webster and Webster, 1977), cat (Cabezudo, 1978), and house mouse (Ehret and Frankenreiter, 1977), the basilar membrane was hypertrophied (i.e., hyalinized). However, no such hyalinization was evident within the basilar membrane of the sloth. Instead, the thickening of the pars tecta and the pars pectinata in the sloth were mainly in the mesothelial layer below the basilar membrane. This mesothelial layer is an integral part of the basilar membrane (Cabezudo, 1978). In the cat, both the mesothelial layer and hyalinization of the

basilar membrane were present (Cabezudo, 1978). Ehret and Frankenreiter (1977) suggested that these thickenings would result in subtle changes in the vibrating patterns of the two components of the basilar membrane, and developed a model of the vibration modes of the basilar membrane using the morphological findings. From that model, they were able to account for the electrophysiological findings on phase opposition between the inner and outer hair cells (Dallos, 1973; Zwislocki, 1975) by the phase opposition movements of the stereocilia of the inner and outer hair cells during displacement. Ehret and Frankenreiter (1977) concluded that inner and outer hair cells have separate modes of mechanical excitation and separate innervation patterns.

MORPHOLOGICAL CONSIDERATIONS OF HEARING

Stimulation of the mechanoreceptors of the cochlea is dependent on the subtle movements of the basilar membrane. If morphological discontinuities exist along the basilar membrane, then these, in turn, would result in an alteration of the mechanical and subsequently the vibration properties of the basilar membrane.

Morphometric studies of the cochlea in some mammals show that the frequencies (particularly high frequencies) to which the mammal is maximally sensitive coincide within the region of morphological discontinuities (Bruns, 1976a, 1976b; Ehret, 1977; Ehret and Frankenreiter, 1977; Ramprasad et al., 1979). In the two-toed sloth, the region of the basilar membrane between 10.5-13.1 mm should thus represent the region where the frequencies to which the sloth is maximally sensitive are analyzed. This suggestion would be strengthened if it can also be demonstrated that within this region, i.e., 10.5-13.1 mm, the vibrating properties of the basilar membrane are different.

Bruns (1976a, 1976b) demonstrated that the ratio of basilar membrane height/width approximates the stiffness gradient of the basilar membrane. In the sloth, the stiffness gradient decreases from the base to about 4.5 mm, where it increases to its maximum stiffness at 10.5 mm and then remains relatively unchanged to 13.0 mm, before declining to the apex (Fig. 13).

Wherever the plateaux of stiffness occurred in the stiffness curves of other mammals, frequencies to which the mammal was maximally sensitive coincided with that region (Bruns, 1976a, 1976b; Ehret and Frankenreiter, 1977; Ramprasad et al., 1979). Frequencies are also expanded within the region of maximum sensitivity (Bruns, 1976b). Therefore, the plateau between 10.5-13 mm in the sloth may be the region where frequencies to which the sloth is maximally sensitive are represented. This region occurs in the upper middle coil, the region of the cochlea associated with low frequencies. It would therefore be of particular importance if it

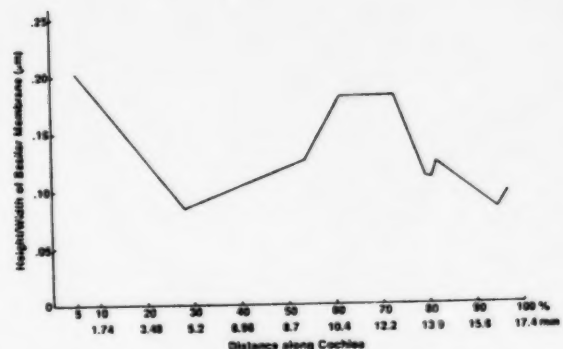


Figure 13. Stiffness gradient along the cochlear length, estimated from the ratio of the height of the basilar membrane to its width. This idealized curve is based on measurements from one sloth. Note; (i) the maximum stiffness occurs at the basal coil, (ii) there is a second area of maximum stiffness within 10.4-13.0 mm from the basal end, (iii) the rapid decline in stiffness at the apex.

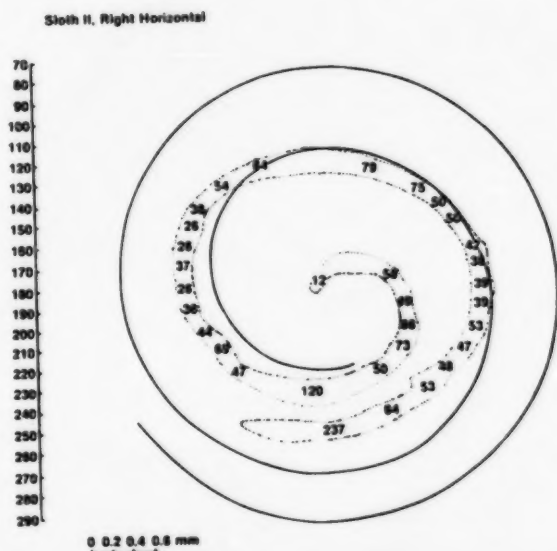


Figure 14. Reconstruction of the coil of the cochlea (procedure of Guild, 1921), with the dotted line showing the course of the spiral ganglion around the cochlea (Ramprasad, 1976). Numbers within the trace of the spiral ganglion are counts of ganglion cells enumerated from a slide of a series that is indicated to the left of the figure. Note; (i) the spiral ganglion includes one and one half turns, (ii) the spiral ganglion starts approximately 0.7 mm from the base of the cochlea and ends approximately 0.3 mm from the apex of the cochlea.

could be demonstrated that the position of maximum amplitude of vibration for the sensitive frequencies coincided within this region of the basilar membrane. Greenwood (1961) derived an equation to relate the critical bandwidth to frequency of vibration or the

position of the maximum amplitude of vibration to the frequency:

$$f = A(10^{ax} - 1) \quad (1)$$

where f = frequency in Hz, A and a are constants having values that are species dependent, and x is the distance along the basilar membrane as measured from the helicotrema (apex) in units of "critical bands" (1 critical band = 1 mm length of basilar membrane). Critical bandwidth is defined by Greenwood (1961) as the frequency interval over which the basilar membrane is effective in spatially integrating the energy of vibration. Eldredge (1974) in his review of the cochlear mechanics of the mammalian ear, suggested that existing data closely agree with Greenwood's (1961) initial assumptions. In *Choloepus*, the range of hearing is considered to be between 0.3-30 kHz (Suga, 1967; Peterson and Heaton, 1968).

By substituting $f = 30$ kHz, the upper limit of the range of hearing in the sloth, into the position/frequency equation and solving for the constant A (with $ax = 0.124 \times 17 = 2.108$) the equation is obtained for the sloth:

$$f = 202.8 (10^{0.124x} - 1) \quad (2)$$

It is now possible to suggest the theoretical position along the basilar membrane x , where the maximum amplitude occurs for frequencies within the range of hearing of the two-toed sloth. In particular, for the frequency of 1.4 kHz, the value $x = 7.2$ mm (or 17.5-7.2 = 10.3 mm from the basal end of the cochlea) is obtained from the equation.

The curve in Fig. 16 demonstrates the theoretical position of maximum amplitude of vibration on the basilar membrane of the frequencies within the range of hearing of the sloth. Frequencies of 0.5-1.5 kHz are represented within 10.2-13.0 mm from the basal end of the cochlea, i.e., the region where morphological discontinuities occur (see Figs. 12 and 13). It is perhaps significant that contact-distress calls of young two-toed sloths were 1.4 kHz (Montgomery and Sunquist, 1974) and that these frequencies are represented within the region of maximum sensitivity of the basilar membrane. These findings suggest the possibility that a fine-tuning mechanism occurs within the basilar membrane itself in the sloth, as has been suggested in bats (Bruns, 1976b; Ramprasad et al., 1979).

Dallos (1970, 1973) has suggested that the larger the size of the helicotrema, the better is the pressure equilibration between the scala vestibuli and scala tympani, since the pressure generated by the travelling waves would fade out earlier as they approach a large helicotrema. The slope of the sensitivity curve became steeper towards the lower frequency limit of hearing as the

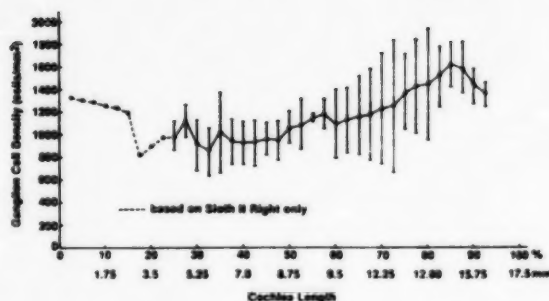


Figure 15. Density of the bipolar ganglion cells along the length of the cochlea. Density is expressed as the mean number of cells per unit cross-sectional area of the spiral ganglion (Ramprasad, 1976; Ramprasad et al., 1979), measured from three temporal bones. Vertical lines show SD. Note: (i) the decrease in density from the base, (ii) the maximum density occurs approximately 15.7 mm from the basal end.

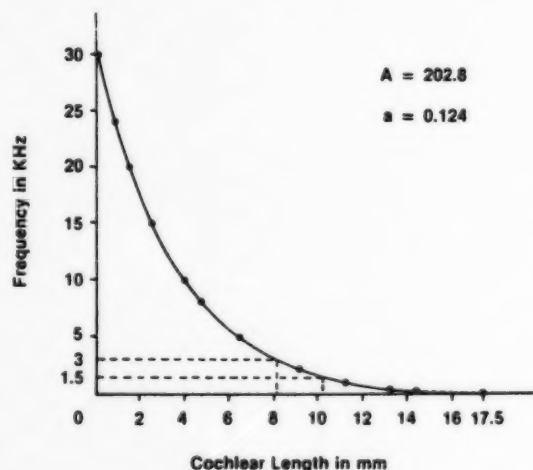


Figure 16. Theoretical frequency map along the cochlear length using Greenwood's (1961) formula for the two-toed sloth. Note: (i) the frequencies below 1.5 kHz are represented between 10.1-13.0 mm from the basal end, (ii) this region coincides with the areas of maximal thickness and cross-sectional area of the pars tecta and pectinata as shown in Fig. 11 and 12, respectively, and within the flat region demonstrating relative stiffness of the basilar membrane in Fig. 13.

helicotrema area increased (Dallos, 1970). In other words, the larger the helicotrema, the lower the low frequency sensitivity of the cochlea. The helicotrema measures 0.325 mm^2 in man (Békésy and Rosenbluth, 1951), 0.152 mm^2 in the cat (Dallos, 1970), and 0.022 mm^2 in the guinea pig (Dallos, 1970). Ehret (1977) showed that the absolute threshold curves in the guinea pig were less steep than in mammals with larger helicotrema (i.e., man and cat). The area of the helicotrema of the sloth was estimated to be 0.25 mm^2 , which is as large as in the guinea pig, the cat, and the house mouse, but not as large as that in man. Peterson and Heston

Table 3: A comparison of cell soma widths and lengths of the vestibular and spiral ganglion, and body mass of representative mammals. Applicable entries are from Alexander (1901), Jones and Spells (1963), Ramprashad et al. (1979), and this study.

Order	Species	Mass (kg)	Vestibular Ganglion Cell Soma (μm)	Spiral Ganglion Cell Soma (μm)
Homo	Man <i>Homo sapiens</i>	70	19 x 27	13 x 15
Artiodactyla	Sheep <i>Ovis aries</i>	48	22 x 32	11 x 16
Carnivora	Dog <i>Canis familiaris</i>	14	19 x 27	8 x 13
	Cat <i>Felis domestica</i>	3.30	16 x 24	9 x 19
Insectivora	Mole <i>Talpa europaea</i>	0.51	14 x 16	8 x 11
	Hedgehog <i>Erinaceus europaeus</i>	0.03	19 x 27	8 x 14
Lagomorpha	Rabbit <i>Oryctolagus cuniculus</i>	0.44	16 x 21	10 x 16
Rodentia	Guinea Pig <i>Cavia cobaya</i>	0.25	19 x 27	11 x 16
	House Mouse <i>Mus musculus</i>	0.02	11 x 16	6 x 8
	Norway Rat <i>Rattus rattus</i>	0.21	16 x 24	8 x 13
Xenarthra	Two toed Sloth <i>Choloepus</i> sp.	3		13 x 17
Chiroptera	Horseshoe Bat <i>Rhinolophus hipposideros</i>	0.01	8 x 13	5 x 9
	Little Brown Bat <i>Myotis lucifugus</i>	0.01	8 x 10	6 x 7

(1968) have shown that the sloth's hearing range is significantly less sensitive than it is in the guinea pig over the entire range of frequencies and requires 10-100 times the sound pressure to produce the standard response. The highest frequency for which the cochlear-microphonic response could be measured was an octave below that of the guinea pig.

The morphometric parameters studied within the sloth's cochlea correlate with the psychoacoustic data. Of significance is the correlation of the frequencies to which the sloth is maximally sensitive with a region of morphological discontinuity along the basilar membrane.

GANGLION CELL DENSITY

The mammalian cochlea is innervated by afferent and efferent nerve systems. The ganglion cell soma of both systems are localized within a bony canal (Rosenthal canal) which spirals around the modiolus (Figs. 3, 4). The afferent ganglion nerve cell is bipolar, with its dendritic end extending outwards to innervate the inner and outer hair cells and its axonal extending centrally to form the cochlear nerve (Bodian, 1962), (Figs. 3, 4). Spoendlin (1968; 1972) has shown that 90 percent to 95 percent of the ganglion cells innervate the inner hair cells while 5 percent to 10 percent of the remaining ganglion cells innervate the outer hair cells in the cat and the guinea pig.

The density of the bipolar ganglion cells in the cochlea of the two-toed sloth decreases from the base where there are 1,300 cells/mm² to 3.0 mm from the basal end where there are 800 cells/mm². The density then increases gradually, attaining a maximum of 1,600 cells/mm² at 13.5 mm from the basal end. The maximum density occurs within the region associated with low frequency vibration, i.e., at the apical region which is also the region where morphological discontinuity of the basilar membrane occurs.

The total numbers of bipolar ganglion cells have been estimated in some mammals; the two-toed sloth has the smallest number of ganglion cells of those studied (Table 2). The total number of ganglion cells is not correlated with body size but rather with the frequency range of hearing in the mammal. Those mammals which utilize high frequencies within their range of hearing have a greater number of ganglion cells as compared to the human. In the sloth, the cell somas measure an average of 13(10-15) μm on its short axis and an average of 17(13-22) μm on its long axis (Table 3). The dimensions of the ganglion-cell soma of the sloth are similar to those in the human despite the apparent disparity in body mass. Cochlear bipolar ganglion cell somas are smaller than those of the vestibular bipolar ganglion cell somas (Table 3).

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